

## Leaf Phenology and Leaf Damage of Saplings in the Luquillo Experimental Forest, Puerto Rico<sup>1</sup>

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### ABSTRACT

Changes in light or water availability can result in synchronous leaf production, concentrating food availability for herbivores of young leaves to only a few months. To determine the importance of food availability on herbivory, leaf phenology and leaf damage were studied in the Luquillo Experimental Forest (LEF) of Puerto Rico. We studied 20 individuals of eight species for two years. Every month, new leaves were marked; the following month, leaf area and area of damage were measured. Over two years, comparison of leaf production and percent herbivory were performed for each species, and for all species taken together. More than 30 percent of the annual leaf production occurred in May and June. Leaf production was associated with an increase in PFD (photon flux density) and was not related to the patterns of rainfall. Although leaf production was synchronous, there were no differences in herbivory between the peak and non-peak periods of leaf production. Possible explanations for the constant levels of herbivory throughout the year are the presence of a generalist herbivore community, the ability of herbivores to track changes in food availability, or high densities of herbivore predators that control herbivore populations.

### RESUMEN

Cambios en la disponibilidad de luz o agua, pueden resultar en una producción sincrónica de hojas, concentrando la disponibilidad de alimentos para herbívoros que consumen hojas jóvenes, en pocos meses. Para determinar la importancia de la disponibilidad de alimento en herbivoría, la fenología de hojas y los daños a hojas nuevas se estudió en el Bosque Experimental de Luquillo (LEF) en Puerto Rico. Estudiamos veinte individuos de ocho especies, por un periodo de dos años. Cada mes, las hojas nuevas se marcaban y el mes siguiente, el área de la hoja y el área de daño se medían. Se compararon la producción de hojas y los porcentajes de herbivoría de los dos años, para cada especie y para las especies tomadas en conjunto. Más de 30 por ciento de la producción anual de hojas ocurrió entre mayo y junio. La producción de hojas se asoció con aumentos en PFD (photon flux density) y no estuvo relacionada con los patrones de lluvia. Aunque la producción de hojas fue sincrónica, no se presentaron diferencias en la herbivoría al comparar el pico de producción con los demás meses. Posibles explicaciones a los niveles constantes de herbivoría a lo largo del año, pueden ser la presencia de una generalistas en la comunidad de herbívoros, la capacidad de los herbívoros de seguir cambios en disponibilidad de alimento o a las altas densidades de depredadores de herbívoros que pueden controlar las poblaciones de herbívoros.

*Key words:* herbivory; leaf production; light availability; Puerto Rico; seasonality; tropics.

LEVELS OF HERBIVORY VARY AMONG FORESTS, and herbivores can consume up to 30 percent of the annual leaf production (Lowman 1992). The major food sources for herbivores are young leaves because of their physical and chemical characteristics (Coley 1983), and these leaves often are produced in synchronous flushes (Lowman 1992, Aide 1993, Murali & Sukumar 1993, Borchert 1994). Synchronous leaf production has been correlated with changes in water or light availability (Lieberman & Lieberman 1984, Wright 1991, van Schaik *et al.* 1993, Borchert 1994, Reich 1994, Wright & van Schaik 1994). In seasonal tropical forests with marked wet and dry seasons, leaf production is pro-

moted when there is a major increase in availability (Wright 1991, Aide 1993). For example, on Barro Colorado Island (BCI), Panama, there is a peak in leaf production at the beginning of the rainy season, when water availability increases (Aide 1993, Barone 1998). When water is not a limiting factor, peaks in leaf production are associated with increases in light availability due to changes in day length or cloud cover in many tropical forests (van Schaik *et al.* 1993, Wright & van Schaik 1994, Coley & Barone 1996, Barone 1998).

Water or light availability can restrict leaf production to certain periods of the year, concentrating food resources for herbivores. This variation in leaf production can cause fluctuations in herbivore populations, leading to differences in levels of herbivory throughout the year (Crawley 1983). It is

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possible that levels of herbivory are low during the peak of leaf production, when there is an increase in food availability, because herbivores are satiated. In contrast, herbivory is high for leaves produced out of the peak, when food is limiting and insect populations are still high (Aide 1993; cf. Lowman 1992).

To determine the effect of food availability on levels of herbivory, we studied patterns of leaf production and leaf damage in the Luquillo Experimental Forest (LEF), Puerto Rico, from November 1994 to October 1996. Two hypotheses were tested: (1) leaf production will be restricted to certain periods of the year and is associated with increases in light availability, because LEF does not have a pronounced dry season and water should not be a limiting factor; and (2) fluctuations in leaf production will affect levels of herbivory; *i.e.*, leaves produced synchronously will receive less damage than leaves produced out of the peak.

## METHODS

**STUDY SITE.**—The study was conducted at the El Verde Research Station (*ca* 57 km<sup>2</sup>; 350 m elev.) in the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico (180°20'N, 65°49'W; Waide & Reagan 1996). The forest is classified as subtropical wet forest, and the dominant tree species are *Dacryodes excelsa*, *Prestoea montana*, *Casuarina arborea*, *Inga laurina*, *Manilkara bidentata*, and *Sloanea berteriana* (Zimmerman *et al.* 1994). The average height of the forest canopy is 20 m and there are few emergent trees (Waide & Reagan 1996). Mean annual precipitation is 3460 mm (McDowell & Estrada-Pino 1988), and although January to April is the period of lowest precipitation, monthly means are usually > 100 mm/mo (Brown *et al.* 1983) and evapotranspiration is lower than precipitation throughout the year (Waide & Reagan 1996). Mean monthly temperatures range between 21 and 25°C. (Brown *et al.* 1983). Rainfall was collected daily on the roof of El Verde Field Station. Light intensity data (photon flux density, PFD) were collected at the Bisley Watershed Experimental Plots (F. Scatena, pers. comm.), which are 8 km east of El Verde Field Station. Data were obtained from a 20-m tower. Even though the study plants were located in the understory, Fernández (1997) found a strong correlation between the yearly pattern of PFD in the understory and canopy at the LEF.

**STUDY SPECIES.**—Two shrubs, *P. riparia* (Rubiaceae)

and *Piper glabrecens* (Piperaceae), and six tree species, *C. arborea* (Flacourtiaceae), *D. excelsa* (Burseraceae), *Guarea guidonia* (Meliaceae), *M. bidentata* (Sapotaceae), *S. berteriana* (Elaeocarpaceae), and *Tabebuia heterophylla* (Bignoneaceae), were studied. These species were chosen because they are among the most common species at this site (Zimmerman *et al.* 1994). For each species, leaf phenology and leaf damage were measured on 20 individuals (1–2 m in height). Plants were located haphazardly in the understory along *ca* 5 km of the La Prieta, upper Sonadora, and Ox Cart Trails. There have been few studies on the herbivore community of the LEF. Lepidoptera, Coleoptera, Orthoptera, and Homoptera (mainly cicadellids) were the most abundant herbivores in the canopy (Schowalter 1994) and understory (Garrison & Willig 1996).

**LEAF PHENOLOGY AND LEAF DAMAGE CENSUSES.**—The study was conducted from November 1994 to October 1995 (year one) and from November 1995 to October 1996 (year two). Each month, all new leaves were counted for determining leaf production, and up to ten leaves per plant were marked with plastic telephone wire to estimate herbivore damage. One month later, leaf area and area damaged were measured on the marked leaves. A plastic grid was used to estimate leaf area to 1.0 cm<sup>2</sup>, and damage was estimated to 0.1 cm<sup>2</sup>. Although this method may overestimate consumption by herbivores and underestimate the effect on leaf area (Coleman & Leonard 1995), there are few alternatives for determining multispecies patterns of leaf damage in tropical forests.

**ANALYSIS.**—For each individual, the monthly proportion of annual leaf production was calculated. For estimating the annual pattern of leaf production for the species, average leaf production of the 20 individuals was determined for every month. Patterns of monthly leaf production for the eight species was computed by averaging the means of each species. Patterns of leaf phenology were compared between years using the Kolmogorov-Smirnov statistic (Ott 1993). Although monthly leaf production within an individual is not independent, by combining the phenologies of many individuals, we feel that the Kolmogorov-Smirnov statistic was an appropriate test for hypothesis one. These data could not be analyzed with repeated measures ANOVA because they were not normally distributed, variances were unequal, and there were many months with no data. We did not combine

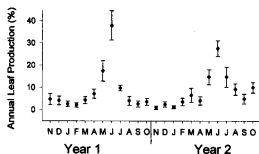


FIGURE 1. Annual leaf production in the LEF Data were collected between October 1994 and November 1996. Error bars represent SD.

data from different months to satisfy the assumptions of the test, because we were interested in monthly variation in phenology. In addition, the Friedman statistic (nonparametric repeated measures statistic) was not used because it ranks data, and thus, information on the cumulative distribution would be lost. Cross correlations were performed to determine if rainfall, light intensity, or day length were important cues for leaf production (Statistix 1996). A maximum lag time of two months was used for this analysis.

Monthly percent leaf damage was calculated for each leaf cohort. Total damaged area on the marked leaves was divided by the total potential leaf area. If a leaf was missing, the average size of the remaining leaves was determined and the area was added to the total area lost and to the total potential leaf area. All species showed a peak in leaf production during May–June, and percent leaf damage was compared between the cohorts produced during the month of peak leaf production and the cohorts produced during the remaining months. The same comparison was made by combining data from all species. In addition, levels of herbivory were compared between years for each species and the eight species combined. The comparison of the levels of herbivory between peak and non-peak periods and the comparison of leaf damage between years were done using the Mann-Whitney *U*-test.

## RESULTS

**LEAF PRODUCTION.**—The overall pattern of leaf phenology (seven species; *T. heterophylla* excluded) differed significantly between years (Kolmogorov-Smirnov = 0.22;  $P = 0.01$ ; Fig. 1). Although the peak in leaf production was in June for both years, the peak was greater in the first year (38%) com-

pared to the second year (28%). There was no significant correlation between rainfall and leaf production in either year (year one:  $R^2 = 0.30$ ,  $P = 0.48$ ; year two:  $R^2 = 0.57$ ,  $P = 0.63$ ). Photon flux density (PFD) was significantly correlated with leaf production in both years. In the first year, PFD during the previous two months had the highest correlation with leaf production (lag of one month:  $R^2 = 0.70$ ,  $P = 0.03$ ; lag of two months:  $R^2 = 0.59$ ,  $P = 0.02$ ). In the second year, a PFD lag of two months had the highest correlation with leaf production (lag of two months:  $R^2 = 0.61$ ,  $P < 0.05$ ).

*Manilkara bidentata* and *S. berteriana* were the species with the most synchronous patterns of leaf production (Fig. 2). In the first year, they produced > 50 percent of their leaves in June, and leaf production was restricted to four to six months. In the second year, the peak of leaf production was less pronounced (*M. bidentata* = 32% and *S. berteriana* = 38%) and leaf production occurred during six to eight months (Fig. 2). For both species, the pattern of leaf production was significantly different between years (Kolmogorov-Smirnov = 0.23;  $P < 0.01$ ).

The peak in leaf production for *P. riparia*, *P. glabrecens*, *C. arborea*, *D. excelsa*, and *G. guidonia* occurred in May or June (Fig. 2). These species produced between 25 and 39 percent of their leaves during the peak month, but there was also leaf production during the rest of the year. Of these species, *P. riparia* was the only species that had different patterns of leaf production between years (Kolmogorov-Smirnov = 0.31;  $P < 0.03$ ). Only two individuals of *T. heterophylla* produced leaves in the first year. All individuals of *T. heterophylla* produced leaves during the second year, and a peak in leaf production occurred in July (41% of total leaf production).

**LEAF DAMAGE.**—Even though few herbivores were directly observed feeding on the study species, the majority of damage was done by chewing insects and a leaf miner on *M. bidentata*. In the first year, leaf damage ranged from  $3.4 \pm 6.1$  percent for *D. excelsa* to  $41.1 \pm 33.4$  percent for *M. bidentata* (Table 1). In the second year, damage ranged from  $2.2 \pm 4.2$  percent for *D. excelsa* to  $37.8 \pm 32.5$  percent for *M. bidentata* (Table 1). Leaf damage was significantly higher during the second year for *P. riparia* (Mann-Whitney *U*-test:  $Z = 2.57$ ,  $P = 0.01$ ), but there were no differences between years for the other species (Table 1). Levels of leaf damage for the all species combined were similar in

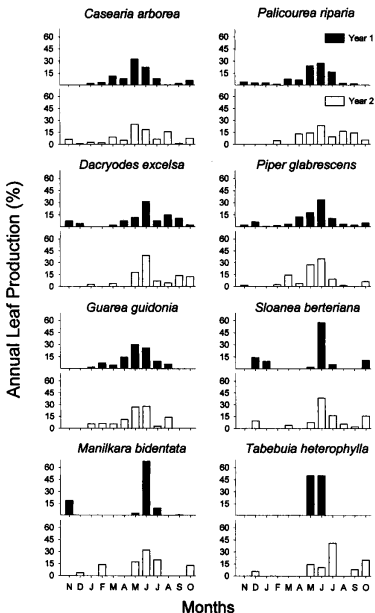


FIGURE 2. Annual leaf production for eight common species in the LEF from year one (November 1994–October 1995) and year two (November 1995–October 1996). In year one, only 2 of 20 individuals of *Tabebuia heterophylla* produced leaves.

both years (year one:  $16\% \pm 11.3$ ; year two:  $15.7\% \pm 10.5$ ).

Levels of damage were similar when comparing leaf cohorts produced during the peak of production and cohorts produced out of the peak (Table 1). *Piper glabrescens* was the only species that had significantly lower levels of leaf damage during the

peak of leaf production in comparison to the rest of the year (Mann-Whitney *U*-test for year one:  $Z = 2.12$ ,  $P = 0.03$ ; year two:  $Z = 2.05$ ,  $P = 0.04$ ; Table 1). When data from all species were combined, there was no difference in levels of leaf damage between the peak in leaf production and the remaining cohorts produced out of the peak

TABLE 1. Mean percent leaf damage ( $\pm$ SD) for each species. Levels of leaf damage during the months of peak leaf production and the remaining months (non-peak). (—) = no data. (\*) Differences between 'peak' and 'non-peak' are significant at  $P = 0.02$  using a Mann-Whitney  $U$ -statistic.

Species	Leaf damage year one	Leaf damage year two	Peak year one	Non-peak year one	Peak year two	Non-peak year two
<i>Casuarina arborea</i>	17.9 $\pm$ 23.2	14.1 $\pm$ 19.2	16.8 $\pm$ 19.8	19.4 $\pm$ 29.6	12.6 $\pm$ 10.5	15.7 $\pm$ 20.3
<i>Dacryodes excelsa</i>	3.4 $\pm$ 6.1	2.2 $\pm$ 4.2	4.3 $\pm$ 8.8	1.9 $\pm$ 4.7	3.5 $\pm$ 6.2	2.6 $\pm$ 4.2
<i>Guarea guidonia</i>	7.2 $\pm$ 16.4	9.8 $\pm$ 10.9	4.7 $\pm$ 9.4	10.9 $\pm$ 19.8	7.9 $\pm$ 4.9	11.0 $\pm$ 11.5
<i>Mamillaria bideniata</i>	41.1 $\pm$ 33.4	37.8 $\pm$ 32.5	46.5 $\pm$ 34.3	33.8 $\pm$ 31.3	41.2 $\pm$ 34.6	36.5 $\pm$ 32.2
<i>Palicourea riparia</i>	14.3 $\pm$ 26.1*	18.2 $\pm$ 21.2*	11.8 $\pm$ 12.2	16.3 $\pm$ 29.3	14.9 $\pm$ 10.3	20.4 $\pm$ 23.4
<i>Piper glaberrimum</i>	11.4 $\pm$ 20.2	12.4 $\pm$ 23.8	5.0 $\pm$ 12.4*	13.9 $\pm$ 25.4*	1.13 $\pm$ 1.8*	12.3 $\pm$ 18.4*
<i>Sloanea berteriana</i>	16.7 $\pm$ 23.2	19.7 $\pm$ 26.0	8.1 $\pm$ 12.4	19.0 $\pm$ 30.3	18.5 $\pm$ 21.0	25.6 $\pm$ 28.3
<i>Tabebuia heterophylla</i>	—	20.6 $\pm$ 37.8	—	—	33.5 $\pm$ 37.6	35.2 $\pm$ 21.6
Community	16.0 $\pm$ 11.3	15.7 $\pm$ 10.5	15.7 $\pm$ 23.9	16.5 $\pm$ 27.3	14.6 $\pm$ 20.5	16.8 $\pm$ 22.6

(Mann-Whitney  $U$ -test for year one:  $Z = 0.4$ ,  $P = 0.7$ ; year two:  $Z = 0.17$ ,  $P = 0.87$ ; Table 1).

## DISCUSSION

Leaf phenology often is associated with seasonality of precipitation (Wright 1991, Aide 1993, Barone 1998) or light (van Schaik *et al.* 1993, Wright & van Schaik 1994, Coley & Barone 1996, Barone 1998). In the LEF, precipitation was not correlated with the pattern of leaf production because there was no strong seasonality in water availability (Waide & Reagan 1996). Leaf production was connected to PFD in the previous two months. In year two, the peak was less pronounced due to lower levels of PFD associated with greater cloud cover during April and May 1996. Even in seasonal forest, light may play a role in leaf production. On BCI, Panama, during the wet season when water is not a limiting factor, variation in light availability has been associated with leaf production (Barone 1998). An important consequence of the seasonality of leaf production is that the majority of food resources for herbivores will be concentrated during a few months.

Aide (1991, 1993) found significantly lower levels of damage on leaves produced during synchronous flushes at the beginning of the rainy season when insect populations were low. In contrast, Lowman (1992) found higher levels of leaf damage during the peaks of leaf production. In the LEF, levels of leaf damage between the peak and the rest of the year were not different for seven of the eight species. The constant levels of leaf damage in the LEF may be a result of herbivores' ability to track changes in leaf production as has been observed at other sites (Wolda 1978, 1992; Basset 1991). Another factor that could contribute to the constant levels of leaf damage is the increase in predator populations (amphibians and anoline lizards) following the peak in leaf production (Reagan 1996, Stewart & Woolbright 1996). An increase in predator density could reduce herbivore density when leaf production decreases. Fluctuations in herbivore populations due to fluctuations in food availability and predator density could explain the constant levels of leaf damage throughout the year, but monthly censuses of insect communities in the LEF are needed to confirm this pattern. Constant levels of leaf damage in the LEF also could be due to a high proportion of generalist herbivores in island ecosystems (Janzen 1973). Generalist herbivores are able to switch among host plants depending on the fluctuations in leaf production. For example, on

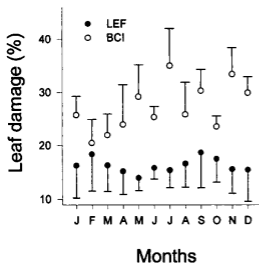


FIGURE 3. Mean monthly leaf damage at the community level at the LEF and BCI. Error bars represent SD.

the island of Grenada, most arthropods are generalists and although leaf production changed throughout the year, the herbivore species composition did not change (Tanaka & Tanaka 1982). Detailed studies on type of herbivores and food preferences will be necessary to test this hypothesis.

Leaf damage on young leaves was lower in the LEF (16.5%) in comparison to BCI (27%; Aide 1993) where the same methodology was used (Fig. 3). A similar pattern of lower leaf damage levels was observed in studies of canopy herbivory. In the LEF, Schowalter (1994) sampled leaves of five species directly from the canopy, and mean leaf damage was ca 1.5 percent. In contrast, levels of leaf damage on fallen leaves at BCI were ca 7.3 percent (Leigh & Windsor 1982). Lower levels of herbivory in the LEF could be related to the high density of herbivore predators: anoline lizards (Reagan 1996) and amphibians (Stewart & Woolbright 1996). The ability of anoline lizards to control herbivore populations has been demonstrated in island ecosystems. In systems where anoline lizards are naturally absent (Spiller & Schoener 1997) or in experiments in which they were removed (Dial & Roughgarden 1995), leaf damage was significantly greater than areas with lizards present. Although different methodologies were used, densities of lizards and frogs were more than an order of magnitude greater in the LEF compared to Panama (Reagan 1996, Stewart & Woolbright 1996; Table

TABLE 2. Frog and lizard densities in the LEF and Panamá.

	LEF	Panamá
Frog density (ind./ha)	20570*	2980** (Panama)
Lizard density (ind./ha)	26085***	1143**** BCI

\* Stewart and Woolbright 1996.

\*\* Inger 1980.

\*\*\* Reagan 1996.

\*\*\*\* Andrews and Rand 1982.

2). The high densities of herbivore predators in the LEF could be associated with the low densities of higher order predators, such as snakes and mammals (Reagan *et al.* 1996). In contrast, on BCI, herbivore predator densities were not as high as in the LEF because there were higher order predators that could control their populations (Andrews 1976, Andrews & Rand 1982). Higher order predators may control lower level predators, and thus release herbivore populations (trophic cascade; Carpenter *et al.* 1985, Power 1990, Pace *et al.* 1998), possibly explaining the lower levels of herbivory in the LEF compared to BCI.

It has been proposed that synchronous leaf production results from the selective pressure exerted by herbivores, because higher levels of herbivory have been observed on leaves produced out of synchrony (Aide 1993). In this study, levels of herbivory were relatively constant throughout the year, which would minimize the potential selective impact of herbivores on leaf phenology. The high density of herbivore predators in the LEF may have been the major factor responsible for the low and constant levels of herbivory. The results of this study support the hypothesis that light is the major factor associated with synchronous leaf production. The change in light availability appears to be an important cue for leaf production in the LEF, but this does not exclude the possibility that variation in light availability also has been an important selective factor shaping the patterns of leaf production (Wright & van Schaik 1994).

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